XXVIII. *Parthenogenesis in Worker Ants, with special reference to two colonies of* Lasius niger, *Linn.* By W. C. Crawley, B.A., F.E.S.

[Read November 1st, 1911.]

It is generally assumed, according to the theory of Dzierzon, that unfertilised eggs of the honey-bee always develop into ♂s, and fertilised eggs into ☿s and ♀s. Eggs laid by worker bees, which have no spermatheca, will therefore produce ♂s only.

This theory has been applied by some authors to ants, without sufficient investigation. It is a well-established fact that ☿ ants lay eggs. Lespès (1863) indeed asserted that such eggs never came to maturity, but Forel (1874) records ☿s of *Formica sanguinea* laying eggs which produced ♂s. Denny showed that ☿s lay eggs, and Dewitz (1879) maintained that the ☿s habitually lay eggs.

Lubbock (1890) carried out careful observations on queenless colonies of *Formica cinerea*, *F. fusca*, *Polyergus rufescens*, and *Lasius niger*, and found that eggs were laid by the ☿s, but only ♂s were produced from these eggs. In colonies of *F. fusca*, and *F. sanguinea* with *fusca* slaves, I have often observed the ☿s to lay eggs, but no ♂s came to maturity in any of the nests, and the *sanguinea* ☿s appeared to devour most of the eggs almost as soon as they were laid. The first indication that eggs laid by ☿ ants might produce ☿s as well as ♂s seems to be in a paper by Reichenbach (1902). Reichenbach obtained some three hundred ☿s and two or three dozen ♂s from the eggs laid by a small queenless colony, containing only a few ☿s, of *Lasius niger*. Mrs. Comstock (Wheeler, 1903), obtained similar results with *L. niger* var. *americanus*.

In a recent paper (1909) Janet criticises Reichenbach's experiment, suggesting that he should repeat it, taking the most minute precautions against error. Janet himself made attempts to obtain ☿s from ☿ eggs with no less than thirty queenless colonies of several species, under

varying conditions and food supply, but in every case where the eggs came to maturity they were ♂s.

On reading these papers it occurred to me that certain hitherto inexplicable phenomena mentioned in a paper some years ago (Crawley, 1900) might be explained by this fact of worker-eggs producing ☿s. In 1896 I had a fair-sized colony of *Lasius niger* in captivity. This colony lost its queen through an accident, soon after the ants were established in their "Lubbock" nest. The queen left a large quantity of eggs. To quote from the above-mentioned paper:—"I had at the time (August 1896) a solitary fertile *Lasius umbratus* queen, and finding that when placed in a pill-box with several *L. niger* ☿s she was not attacked, I put her into the queenless nest of *L. niger*. . . . The little black ants received her eagerly, and she was very shortly established as queen of the nest. . . . During the year 1897 all the eggs and larvae left by the old *niger* queen hatched, the last brood of larvae having lived through the previous winter, *but in that year and the next*, though I paid careful attention to the nest, *I was unable to trace any of the offspring of the L. umbratus queen to maturity.* As the ☿s of *L. umbratus* are bright yellow, and those of *L. niger* are black, there is no possibility of confusing the two." I may mention that I had observed the *umbratus* queen lay eggs during 1897, and numbers of larvae lived through the winter of 1897–8, yet during 1897 and 1898 all the ants (several hundred ☿s) that reached maturity in the nest were *L. niger*. The *niger* ☿s must therefore have devoured the *umbratus* eggs or larvae, which is not surprising, since in 1899, when the *umbratus* eggs were at last allowed to reach maturity, the young ☿s were all killed and eaten, or divided among the larvae as food, by the *niger* ☿s, within a few days of hatching. The queen used to spend a long time licking the eggs and larvae, an unusual proceeding for a queen ant.

At the end of the paper I wrote that this acceptance of an alien queen by a queenless colony of another species might throw some light on the origin of slavery among ants. This has now been demonstrated by Wheeler and Wasmann.

In another paper (Crawley, 1909) before describing the second similar case of *L. niger* and *umbratus* of 1908, I recapitulated the principal facts of the 1896 colony, with a few important additions from my notebook:—"No eggs

were laid by the queen in 1896 (in my experience the ♀s of *L. umbratus* do not lay till the year following impregnation), and the *niger* larvae left by the old queen lived through the winter and began to change into pupae at the beginning of June 1897. On June 26th the *umbratus* queen began to lay, and by August 1st there was a large quantity of eggs laid by her" (and also, as the results show, by the *niger* ☿s). "The larvae from these eggs lived through the winter. On May 31st, 1898, the first larva in the nest changed into a pupa, and by the end of July there were about one hundred pupae in the nest. On August 2nd twenty pupae hatched, the young ants all being *L. niger* ☿s." This result being inexplicable to me, as I took it for an established fact that if eggs had been laid by the *niger* ☿s the resulting perfect insects would have been ♂s, I tried to explain it by assuming an error in my records, as follows:—"It is clear that there is an error in my records here, for it is hardly possible that larvae from *niger* eggs laid in 1896 could have lived till 1898 before completing their metamorphoses. I have recorded giving the nest some *niger* pupae on August 6th, but some must have been given to the nest before August 2nd." However, in view of the identical results obtained with the other similar colony from 1908 to 1910, where there was no possibility of error, I think that there was no mistake here, and that the results were due to parthenogenetic eggs laid by the *niger* ☿s producing ☿s. The following year, 1899, hundreds of *L. umbratus* ☿s came to maturity in the nest, and were all, as stated above, killed by the *niger* ☿s. No *niger* ☿s appeared after 1898. In 1900 the *umbratus* ☿s began to hatch in July, and this time were not molested by the *nigers*, and by July 18th there were twenty alive and carrying pupae about the nest. This interesting colony unfortunately came to an untimely end, as I was obliged to leave it in other hands for more than two months, and found on my return all the ants dead except the queen, who died shortly afterwards. There was not a single *niger*, or remains of one, to be found in the nest, though there were hundreds of dead *umbratus* ☿s.

During the four years this colony was in my possession *not a single ♂ of either species made its appearance.*

Again, in September 1908, I had a queenless colony of *L. niger* which accepted a fertile *umbratus* ♀ as queen on September 19th. I was determined that there should be

no possibility of any error in this case, and the most careful records have been kept. This colony had no brood of any kind, so to occupy the numerous ☿s I gave them some *niger* eggs. All these eggs became larvae before November 1908, and no eggs were laid by the *umbratus* queen or the *niger* ☿s during that year. By the end of April 1909 most of these *niger* larvae were more than half-grown, and a few nearly ready to pupate, and on May 4th there were seven eggs in the nest. I did not see them laid, so was not certain whether they were workers' or the queen's eggs. On May 7th, however, the abdomen of the queen was considerably swollen, and I observed her in the act of laying. From this time till late in June I repeatedly saw her depositing eggs, though I never succeeded in seeing a *niger* ☿ doing so. The first *niger* larva pupated on May 12th, and on the 30th there were over fifty pupae. The queen was often seen to lick the eggs herself, but none hatched till June 20th, when I observed a number of very small larvae. This was about six weeks after the first eggs were laid.

On June 25th there was a fair number of these small larvae side by side with the eggs. From July 11th till August 9th, 1909, the nest was under the care of Mr. A. H. Hamm, of the Oxford University Museum, who took special care that no eggs, larvae or pupae of any species were introduced into the nest. On August 9th, when I took back the nest, the queen had apparently ceased to lay, as her abdomen was its normal size; and there were numbers of larvae of all sizes, a few changing into pupae, and several newly-emerged *niger* ☿s. I observed numbers of *niger* ☿s hatch daily till August 24th, by which time there could have been very few, if any, of the last year's *niger* larvae which had not already pupated, as all the remaining larvae in the nest were small. From August 24th till October 3rd, 1909, during my absence in America, Mr. Hamm again most kindly took charge of the nest, and assures me that no young of any species of ant was put into the nest.

The nest contained, on my return, many half- and three-quarter-grown larvae (in which condition they passed the winter), a few pupae, and a large quantity of eggs, much larger than had been in the nest on August 24th. As the queen had to all appearance ceased laying by that date, many of these eggs may have been laid by the *niger* ☿s.

There was no sign of *umbratus* ☿s. The last pupa came to maturity on October 22nd, 1909, and was a *niger* ☿. No males had appeared.

The colony passed the winter of 1909–10 in good condition, the larvae, as usual, remaining unchanged in size till the beginning of April 1910. On the 5th of that month one larva was nearly full-grown, but it was not till May 22nd that eleven larvae spun their cocoons. The following day this number had increased to twenty, and to more than sixty on the 24th.

The *umbratus* queen began to lay again on May 26th, some three weeks later than the previous year, but she laid many more eggs, and her abdomen became greatly distended.

Finally, on July 2nd, 1910, the first pupae hatched. There were six newly-hatched ☿s of a pale grey colour at 11.25 p.m. The following day the young ants had not quite attained their full colour, but they were unmistakably *niger*. On July 7th there were between fifty and sixty newly-hatched ☿s, none being *umbratus*. On the 17th I took a number of these young ☿s, some still pale, and some nearly full-coloured ones, and a few of the old *niger* ☿s, and sent them to Dr. Forel for identification. A few days later I received an answer from him stating that all the ants I had sent him were *Lasius niger purus*, and drawing my attention to Reichenbach's paper mentioned above.

By August 14th, 1910, all the pupae had hatched, and there were about 100–200 eggs, many small larvae, and two or three half-grown larvae. All the new ☿s were of a uniform size, somewhat smaller than the normal *L. niger*.

During last autumn I talked the matter over with Mr. H. Donisthorpe, who kindly communicated with Father Wasmann. In his reply, Wasmann suggested having some of the ☿s dissected to see if any of them possessed a *receptaculum seminis*. Mr. G. H. Grosvenor, of the Oxford University Museum, very kindly undertook this task, and dissected twelve ☿s of various sizes from the colony. In none of them was there a *receptaculum seminis*.

There can be little doubt that we have to deal here with a genuine case of parthenogenesis, confirming Reichenbach's experiment, and helping to prove that eggs laid by ☿s of some species can produce ☿s and not ♂s. It is note-

worthy that not a single ♂ has been produced in either colony.

The further history of this colony, together with that of the former one, tends to show that the egg-laying capacity of the ☿s is not of very long duration, lasting two seasons at most, while the life of the ☿ may be from three to seven years.

The first eggs of this year were laid on May 10th, sixteen days earlier than in 1910, and the first larva (from last year's eggs) reached the pupal stage on May 30th, and on June 7th there were about fifty pupae. On July 11th I found four callows in the nest, all of a yellow colour, and unmistakably *L. umbratus*. On the 15th there were over thirty. By July 27th this number had increased to over one hundred, and there was no sign of any hostility towards them on the part of the *niger* ☿s.

It is curious that while the young *umbratus* ☿s devoted their attention almost entirely to the care of the larvae, the *niger* ☿s alone surrounded the *umbratus* queen.

At the present moment (October 12th, 1911), the *umbratus* ☿s, as far as can be judged, slightly outnumber the *nigers*, and the latter still pay more attention to the queen than the ants of her own species. Not a single *niger* has hatched in the nest this year. From the number of the larvae, presuming these to be exclusively *umbratus*, as is almost certain, the *niger* population of the colony will be outnumbered by at least four to one next year.

Allowing for the increased mortality among the more active *niger* in nature, it would seem that it takes four to five years for a colony founded in this way to become exclusively *umbratus*. In this particular colony the total number of deaths from natural causes among the *niger* from September 1908 to September 1911 was 416, and there are still over 300 *niger* ☿s alive in the nest.

It has been suggested by Wheeler (1909) that the usual sterility of ☿s is influenced by their being constantly in a state of semi-starvation, nearly all the food they obtain being given to the larvae. Thus in the second colony (No. 2) the workers were without larvae to tend from July to October 1908, and therefore all the food was consumed by them. But in the first colony (No. 1) this was not the case, as the nest contained larvae from the first.

It appears also that in certain species when a colony is deprived of its queen several workers become fertile. It

is possible that the presence of an alien queen with delayed fertility might bring about a similar result, since the queens of *L. niger*, which found their nests themselves, begin to lay a few days after impregnation, whereas the queens of *L. umbratus* do not lay for eight or nine months after.

I wish here to express my cordial thanks to Mr. Donisthorpe for his valuable help with the bibliography, and in getting the dissections done. The latter was of great importance, as it proved that the ♀s could not have been fertilised.

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